

Changes in tree abundance over 15 years at Otari: Succession or possum control?

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Abstract

We assessed changes in the abundance of adult trees in a conifer-broadleaved forest on the North Island over a 15-year interval. All woody plants (> 3.6 m tall) were censused in six plots (30 x 30 m²) in 1993 after a sustained period of elevated possum abundance. The plots were then resurveyed in 2008, following 15 years of continuous possum control. Results showed that overall tree abundance increased between censuses. However, community-level increases in only the two most abundant species, *Dysoxylum spectabile*, and to a lesser extent *Macropiper excelsum*, were observed. Temporal changes in species richness were not observed. Although 15 years is a relatively short time period, results suggest possums have a relatively simple effect on adult tree communities, which results from the suppression of numerically dominant species.

Keywords: Brush tail possum - *Dysoxylum spectabile* - forest structure - species richness - species diversity.

Introduction

Like many isolated islands, New Zealand lacks native mammals, aside from two species of bats. Consequently, the New Zealand flora has evolved in absence of mammalian selection pressures and most New Zealand plant species lack defensive structures such as spines and thorns which in other parts of the world offer protection against mammalian herbivores (Kuhajek *et al.* 2006). Since human arrival, many herbivorous mammals have been introduced to New Zealand, which may have a deleterious effect on native

forests. Introduced mammals can have negative effects in plant communities (Cunningham 1979; Campbell 1990; Payton 2000; Pechelaring & Batcheler 1990; Rose *et al.* 1993; Rogers & Leathwick 1997; Bellingham 1999; Nugent *et al.* 1997). Arguably the most destructive introduced mammal species is the brush-tail possum (*Trichosurus vulpecula*), which is now the most abundant browsing animal in New Zealand (Nugent *et al.* 2001). However, the effects of herbivores on forest structure may be complex and additional research is needed to precisely identify the effects of

introduced mammals, and in particular brush-tail possums, on New Zealand forest structure.

Previous work has generated invaluable insight into the effects of possums on native New Zealand plants (see Montague 2000). Studies have identified how introduced mammals can affect individual plant species (Cowan 1991; Rogers & Walker 2005; Ulrich & Brady 2005; Nugent *et al.* 2002; Sweetapple *et al.* 2002) and individual life stages, particularly seedlings (Wilson *et al.* 2003; Blick *et al.* 2008; Clayton *et al.* 2008). Fewer studies have investigated entire plant communities (Owen & Norton 1995; Cochrane *et al.* 2003; Sweetapple *et al.* 2004; Jacometti *et al.* 2007). Therefore, additional study of entire communities of adult trees is needed to fill key gaps in our understanding of the effects of possum control on native plant communities.

We quantified changes in forest structure in Otari-Wilton's Bush. Six permanent plots, which encompassed 5,400m² of mature forest, were censused before and 15 years after an extensive possum-poisoning program. Changes in tree density and tree species richness were assessed to evaluate how forest structure has changed since the initiation of the possum control program.

Methods

Study site

Otari-Wilton's Bush (41°14' S, 174°45' E) is located just within Wellington city limits at the southern tip of the North Island of New Zealand, and encompasses approximately 100 ha of native forest. The reserve is situated 70-280 meters above sea level and the soil is comprised of stoney colluvium of greywacke parent material. Average annual rainfall totals 1,240 mm and

average daily temperatures range from 20 °C in summer to 7 °C in winter (Otari Native Botanic Garden and Wilton's Bush Reserve 2007). The vegetation is classified as coastal conifer-broadleaved forest, whose vertical structure is highly complex and similar to most tropical forests (Dawson 1988). It has a fairly continuous canopy, which is frequently interrupted by canopy gaps and canopy emergent tree species. A dense community of shrubs and tree ferns occurs beneath the canopy (Blick *et al.* 2008). Lianas and epiphytes are also abundant (Burns & Dawson 2005). *Dysoxylum spectabile* is the dominant canopy-forming species, alongside *Melicytus ramiflorus*, *Corynocarpus laevigatus* and *Eleaocarpus dentatus*. *Macropiper excelsum* and *Geniostoma rupestre* are the most common subcanopy shrubs. Emergent trees include *Dacrydium cupressinum*, *Beilschmedia tawa* and *Knightia excelsa*. Burns (2007) gives a detailed inventory of the woody plant community.

Data collection

Six permanent forest plots, each measuring 30 m x 30 m, were established by Marjot (1992) in different parts of the reserve prior to possum control. One plot encompasses undisturbed, old-growth forest located on a shallow, north-facing slope. A second, similarly undisturbed plot faces has an easterly aspect. The four remaining plots have a more southerly aspect and were all pasture prior to 1900. These four plots have therefore undergone secondary succession for over a century.

In response to complaints by local residents living close to Otari Wilton's Bush, whose gardens and even homes were being invaded by possums, the Wellington City Council initiated a major possum control program in 1993 (Otari

Native Botanic Garden and Wilton's Bush Reserve 2007). It was estimated that between July 1994 and June 1996, after the establishment of 50 poisoned bait stations, over 1,000 possums were eliminated. Only five possums were eliminated after a more intensive poisoning program in November 1998 (see O'Leary 1999). Periodic poisoning has been conducted since and possum numbers have remained at nearly undetectable levels.

In January-February 2008, following 15 years of possum control, all six permanent forest plots were recensused. All vascular woody plants with diameter at breast height ≥ 10 cm were individually marked with permanent metal tags and their heights were measured with either a collapsible ruler or clinometer. This study focuses on trees taller than 3.7 m, which were divided into two height classes (3.7 m - 7.5 m and > 7.5 m) following Marjot (1992).

Data analyses

Four analyses were conducted to test for changes in tree density and species richness between censuses. First, non parametric Wilcoxon tests were used to establish differences in the population density of each plant species between 1993 and 2008. A non-parametric

approach was adopted because data for most species could not be normalized. Second, repeated measures analysis of variance was used to test for community-level differences in total plant density between censuses. For this analysis, total plant densities (all species combined) in each plot were used as the dependent variable. Time (1993 and 2008) was treated as a repeated measure and height class (3.7 m - 7.5 m and > 7.5 m) was treated as a fixed factor. Third, to test for differences in tree species richness per unit sampling area between censuses, the total number of species present in plots was compared with a paired sample t-test. Data conformed to assumptions without transformation. Fourth, rarefaction analyses were used to compare species richness per plant sampled, rather than per unit area. For rarefaction analyses, data were pooled among plots within each census and the cumulative number of tree species encountered per plant sampled was compared. A rarefaction curve relating the number of species encountered to the number of plants sampled (along with a 95 % confidence interval) was constructed via a computer simulation, which randomly sampled plants from the total pool available to obtain an expected species richness per

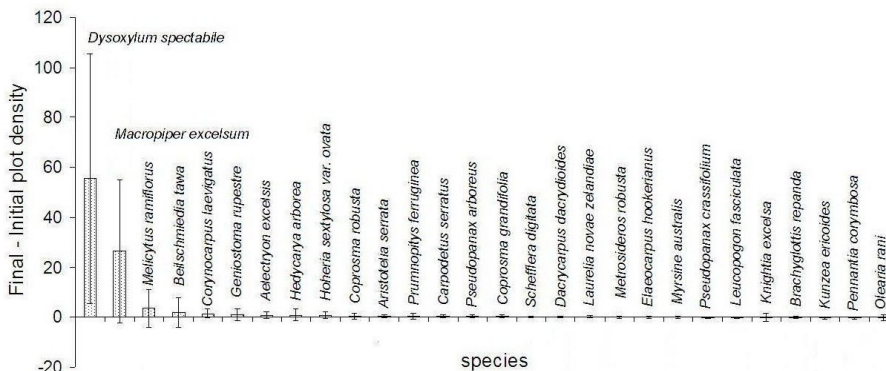


Figure 1. Difference in abundance for each plant species between censuses (\pm SE).

plant sampled. Rarefaction analyses were conducted using *rarefact* 1.0 software following Blick *et al.* (2008). All other analyses were conducted in SPSS (2006).

Results

The most abundant species in the community, *Dysoxylum spectabile*, increased in abundance between censuses ($Z = -0.201$, $P = 0.028$). The second most abundant species, *Macropiper excelsum*, showed marginal increase in density ($Z = -1.892$, $P = 0.058$). No other species differed in density between censuses ($Z > -1.60$, $P > 0.109$ for all, Figure 1). Total plant densities increased between censuses ($F_{1,10} = 15.680$, $P = 0.003$), but not between size classes ($F_{1,10} = 0.690$, $P = 0.425$). A weak interaction was observed between time and height class ($F_{1,10} = 4.338$, $P = 0.064$), indicating that smaller trees showed a slightly higher increase in density between censuses than larger trees (Figure 2). Species richness per unit area did not differ between censuses ($t = -2.038$, $P = 0.097$, Figure 3). Similarly, rarefaction analyses also indicated that species richness did not differ between censuses (Figure 4).

Discussion

Forest structure in Otari-Wilton's Bush changed over the 15 year census interval. However, these changes were relatively simple and resulted from increasing abundance of the most common species, *Dysoxylum spectabile*, and to a lesser extent, *Macropiper excelsum*. Abundances of all other species remained almost unchanged between censuses. Changes in species richness, regardless of how it is measured, were not observed.

Increases in the abundance of *Dysoxylum spectabile* and *Macropiper excelsum* could result from enhanced recruitment since the removal of possums. Merret *et al.* (2002), Nugent *et al.* (2002) and Buddenhagen & Ogden (2003) also found that *D. spectabile* is highly susceptible to possum browse and that this species increases markedly in abundance following possum control. Ogden & Buddenhagen (1995), who investigated a possum-browsed *D. spectabile* forest on the Coromandel Peninsula, found that the basal area of *D. spectabile* declined by 51-58 % and that vegetation biomass declined by 5-20 % over a 10-year period. In the absence of possum browse, seed-

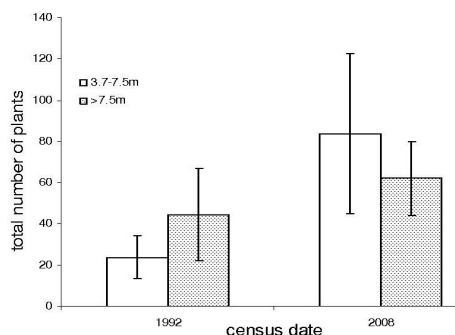


Figure 2. Average abundance (\pm SE) of pole (3.61-7.5 m) and adult (> 7.5 m) trees.

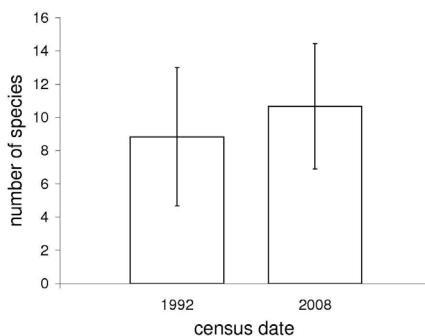


Figure 3. Average number of species (\pm SE) found during each census.

lings present during the initiation of possum control may have experienced higher probabilities of recruitment. Possums are also known to suppress fruit production and reproductive output of native New Zealand trees (Cowan & Waddington 1990). Therefore, the sharp increases in *D. spectabile* abundances could also be due to the release from possum seed predation. Less is known about the effects of possums on *Macropiper excelsum*, but similar circumstances may apply to this species. Somewhat differently, possums may not have a preference for particular plant species and instead consume plants in relation to their abundance in the community, resulting in a disproportionately negative effect on the two most abundant species.

In a similar study less than 2 km away in the Karori Wildlife Sanctuary (KWS), Blick *et al.* (2008) found somewhat different results. They too found that *D. spectabile* responded increased in abundance after mammal exclusion. However, they also documented that a large number of other tree species changed in abundance; some species increased in abundance fol-

lowing mammal exclusion, while others decreased in abundance. Differences between studies may result from several factors. First, two plots in Otari Wilton's Bush are in old-growth forest, while the other four plots are in the later stages of succession. All plots located in KWS are undergoing succession, and are also at earlier stages of regeneration. Thus, differences in the results between studies may therefore result from differences in the successional status of each locale. Second, all mammals except for mice have been completely excluded in KWS by a predator-proof fence. Mammals have not been completely eradicated from Otari-Wilton's Bush and many other types of mammals (e.g. rats) may influence the plant community. Therefore, the simpler changes in forest structure observed in Otari-Wilton's Bush may result from less complete mammal eradication. Lastly, many native bird species that perform important roles as pollinators and seed dispersers have been reintroduced in KWS. Although several avian pollinators and seed dispersers are common in Otari-Wilton's Bush (e.g. tui, *Prosthemadera novaeseelandiae* and kereru, *Hemiphaga novaeseelandiae*), differences in long-term vegetation change between locales might also result from differences in the abundance and species composition of avian mutualists. On the other hand, a strong similarity between Blick *et al.* (2008) and this study was that species richness did not change.

Although results seem to implicate possums as the causal factor responsible for observed changes in forest structure, our data cannot exclude other causal processes as explanations for changes in forest structure. For example, changes in climate over the past 15 years (Wratt *et al.* 2007) may have contributed to the increased dominance of *D. spectabile*.

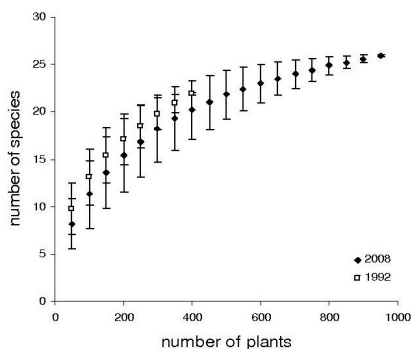


Figure 4. Rarefaction curve of number of individual plants against number of species (\pm 95% CI). The density of plants increased by more than twofold from 1992 to 2008. However, the number of species remained almost the same.

Spatial and physical features of the plots may also have affected results. Four of the surveyed plots were similarly located on south-facing slopes, which differ environmentally from north-facing plots (Calaway & Walker 1997; Merret *et al.* 2002). While the spatial extent of sampling is much larger than recent studies (e.g. Blick *et al.* 2008), whether the results from these plots accurately reflect dynamics throughout the reserve is unclear. The four south-facing plots are also undergoing succession, so the increasing abundance of *D. spectabile* may be part of the natural successional sequence. However, the increase in *D. spectabile* was observed in both old growth plots and plots undergoing secondary succession (see Appendix I).

Fifteen years is a short time interval to evaluate temporal changes in forest composition, given that most forests are expected to turn over every 75-150 years (Hartshorn 1980). However, over this relatively short time period, several changes in Otari-Wilton's Bush were observed. Several of the most abundant species increased in abundance, and these increase coincided with an extensive possum removal program. Results from this study therefore suggest that possums have a relative simple effect on this tree community, by reducing the abundance of the dominant species. Additional work on forests in other parts of New Zealand is needed to precisely determine the long-term effects of possum browse on New Zealand forests.

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Appendix I. Plots 1 and 6 are old growth, undisturbed plots. Plots 7, 12, A and B are undergoing secondary succession for over 100 years.

Quadrat	Species	1992	2008
1	<i>Aristotelia serrata</i>	0	1
1	<i>Beilschmiedia tawa</i>	14	13
1	<i>Carpodetus serratus</i>	0	2
1	<i>Coprosma robusta</i>	0	4
1	<i>Corynocarpus laevigatus</i>	0	3
1	<i>Dacrydium cupressinum</i>	7	5
1	<i>Dysoxylum spectabile</i>	0	5
1	<i>Elaeocarpus dentatus</i>	4	2
1	<i>Elaeocarpus hookerianus</i>	1	1
1	<i>Geniostoma rupestre</i>	4	1
1	<i>Hedycarya arborea</i>	0	4
1	<i>Knightia excelsa</i>	4	5
1	<i>Kunzea ericoides</i>	2	0
1	<i>Leucopogon fasciculatus</i>	1	0
1	<i>Macropiper excelsum</i>	4	2
1	<i>Melicytus ramiflorus</i>	11	28
1	<i>Metrosideros robusta</i>	1	1
1	<i>Myrsine australis</i>	1	1
1	<i>Olearia rani</i>	1	0
1	<i>Pennantia corimbosa</i>	1	0
1	<i>Prumnopitys ferruginea</i>	3	4
1	<i>Pseudopanax arboreus</i>	0	2
1	<i>Pseudopanax crassifolius</i>	1	0
6	<i>Beilschmiedia tawa</i>	13	14
6	<i>Dysoxylum spectabile</i>	64	105
6	<i>Geniostoma rupestre</i>	0	8
6	<i>Hedycarya arborea</i>	7	5
6	<i>Laurelia novae-zelandiae</i>	0	1
6	<i>Macropiper excelsum</i>	1	6
6	<i>Melicytus ramiflorus</i>	3	10
6	<i>Pittosporum eugenioides</i>	0	1
7	<i>Aristotelia serrata</i>	0	1
7	<i>Beilschmiedia tawa</i>	5	13
7	<i>Corynocarpus laevigatus</i>	1	6
7	<i>Dacrycarpus dacrydioides</i>	0	1
7	<i>Dysoxylum spectabile</i>	5	98

Appendix I continued.

Quadrat	Species	1992	2008
7	<i>Hedycarya arborea</i>	0	1
7	<i>Laurelia novae-zelandiae</i>	1	1
7	<i>Macropiper excelsum</i>	2	13
7	<i>Melicytus macrophyllus</i>	0	4
7	<i>Brachyglottis repanda</i>	1	0
7	<i>Melicytus ramiflorus</i>	2	1
12	<i>Beilschmedia tawa</i>	1	8
12	<i>Brachyglottis repanda</i>	1	1
12	<i>Coprosma grandifolia</i>	0	2
12	<i>Dacrycarpus dacrydiodes</i>	1	2
12	<i>Coprosma robusta</i>	1	0
12	<i>Dysoxylum spectabile</i>	43	170
12	<i>Geniostoma rupestre</i>	1	2
12	<i>Hedycarya arborea</i>	3	7
12	<i>Knightia excelsa</i>	1	1
12	<i>Macropiper excelsum</i>	4	34
12	<i>Melicytus ramiflorus</i>	4	6
12	<i>Schefflera digitata</i>	0	1
12	<i>Beilschmedia tawa</i>	1	0
12	<i>Pennantia corimbosa</i>	1	0
A	<i>Beilschmedia tawa</i>	19	17
A	<i>Corynocarpus laevigatus</i>	1	1
A	<i>Dysoxylum spectabile</i>	49	66
A	<i>Elaeocarpus dentatus</i>	4	3
A	<i>Geniostoma rupestre</i>	2	0
A	<i>Hedycarya arborea</i>	2	2
A	<i>Knightia excelsa</i>	1	1
A	<i>Macropiper excelsum</i>	3	5
A	<i>Melicytus ramiflorus</i>	11	10
A	<i>Olearia rani</i>	4	1
B	<i>Beilschmedia tawa</i>	3	2
B	<i>Corynocarpus laevigatus</i>	0	1
B	<i>Dysoxylum spectabile</i>	55	105
B	<i>Geniostoma rupestre</i>	0	2
B	<i>Hedycarya arborea</i>	0	1
B	<i>Knightia excelsa</i>	3	1
B	<i>Macropiper excelsum</i>	10	35
B	<i>Melicytus ramiflorus</i>	16	14
B	<i>Prumnopitys taxifolia</i>	0	1